Plant Utilization Patterns of a Guild of Leafhoppers on a Woody Plant Community in the Chihuahuan Desert

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ABSTRACT We examined plant use versus plant availability by a leafhopper guild from a Chihuahuan Desert plant community. Some native woody plants species of the Chihuahua Desert behave as weeds (e.g., *Gutierrezia* spp.) and could be subjects of augmentative biological control. As a first step, we wanted to know how the leafhopper guild used the woody plant community in the Chihuahua Desert to identify possible candidates to be studied. At least 37 leafhopper species were sampled on 13 woody and perennial plant species. Individual plants were sampled with sticky-traps on nine dates from June 1997 to July 1998. Leafhopper counts and plant availability were used to determine if leafhoppers used plants in proportion to their availability. Analysis of the 13 most abundant leafhopper species indicated differential use of at least one or more plant species in proportion to plant occurrence. Approximately 40% of all possible plant-insect pairs (169 pairs, 13 plants, and 13 insects) demonstrated under-utilization of plants (less than expected) by the leafhoppers. Nearly 50% of the pairs demonstrated plant use in proportion to their availability (random utilization), and in only 10% of pairs, leafhoppers used plants more often than expected. In our study site, 66.7% of the leafhopper species exhibited preference for one or two plant species, whereas the remaining 33.3% exhibited no preference for any studied plant. Our plant utilization results reaffirm published available host plant records for the leafhoppers analyzed. Qualitative temporal patterns in plant utilization were not detected. Specialist species exhibited different host uses in response to increasing leafhopper abundance. At seasonal peak abundance, specialist leafhoppers showed two different strategies: leafhoppers increased their preference toward their preferred host plants, and leafhoppers decreased their preference toward their preferred plants. The possible use of this methodology for augmentative biological control is discussed.

KEY WORDS Cicadellidae, leafhoppers, desert plants, host availability

EVERY HERBIVOROUS INSECT species is associated with a host plant range, which can be of a single or several plant species. However, host ranges can fluctuate in ecological time because food availability is not continuous in time and space, resulting in differential plant use. Even plants of the same species may differ in their quality as hosts: neighboring plants may be differently attacked; one plant may be severely damaged while others remain undamaged (Mopper and Simberloff 1995). Plant resources are combined in many ways producing various arrays of nutritional, and/or defense chemistry quality and quantity (Wiens 1976, Jones 1983).

Plant utilization can be measured in several ways. Host plant range is one measure commonly used to categorize insect species as generalists or specialists. However, researchers often do not describe the method used to rank insect species as generalists or specialists, or only include the insect in a category using the author's own criteria (Claridge and Wilson 1976, Cates 1980, Schultz 1981, Marques et al. 2000). There is no agreement about why the proportion of specialized insects (50%) is more frequent than expected (Futuyama and Gould 1979, Bernays and Graham 1988). Claridge and Wilson (1978) defined three levels of phytophagy (monophagous, oligophagous or polyphagous) based on the number and degree of relatedness of plant species used by an insect species. Interactions between phytophagous insects and host plants can result in nonrandom patterns of plant utilization.

Several researchers have sought biological explanations for the observed patterns (Barbosa 1988, Bernays and Graham 1988, Jansen 1988, Rausher 1988, Schultz 1988). Insect patterns of host utilization result from an insect's host plant range, plant condition and availability, natural enemies' action, other possible biotic interactions, like competition, endophytes, and environmental conditions. Studies in insect-host plant relationships have been made using field records, plant utilization studies in the field and host preference

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Table 1. List of the 13 plant species used in the study

Scientific name	Common name	Family	Architecture and size
Brickellia laciniata Gray	Cutleaf brickellbush	As	Shrub of 1-2 m
Fourensia cernua DeCandolle	Tarbush	As	Shrub of 1-2 m
Gutierrezia sarothrae (Pursh) Britton and Rusby	Broom snakeweed	As	Woody plants 0.2-1 m Treated as one species
G. microcephala (DeCandolle) Gray	Threadleaf snakeweed	As	Woody plants 0.2-1 m
Melampodium leucanthum Torrey and Gray	Blackfoot daisy	As	Perennial 10-3-cm
Parthenium incanum Humboldt, Bonpland, & Kunth	Mariola	As	Woody perennial 0.4-1 m
Thymophylla acerosa (DeCandolle) Strother	Prickleleaf dogweed	As	Shrubby perennial 10-25 cm
Zinnia acerosa (DeCandolle) Gray	Desert zinnia	As	Low shrublet 6-25 cm
Dalea formosa Torrey	Feather indigobush	Fa	Shrub 0.3-1 cm
Prosopis glandulosa Torrey	Honey mesquite	Fa	Shrub or tree up to 4 m
Croton pottsii (Klotzsch) Mueller of Aargau	Leatherweed	Eu	Perennial of 20-60 cm
Rhus microphylla Engelmann	Littleleaf sumac	An	Shrub of 1-3 m
Yucca elata Engelrnann	Soap-tree yucca	Ag	Semi-succulent shrub up to 5 m
Larrea tridentata (DeCandolle) Coville	Creosote-bush	Zy	Evergreen bush of up to 2 m

Information for this study was taken from Allred (1988). As, *Asteraceae;* Fa, *Fabaceae;* Eu, *Euphorbiaceae;* An, *Anacardiaceae;* Ag, *Agavaceae;* Zy, *Zygophyllaceae*

studies in the lab. Host records taken in the field were traditionally rejected due to their lack of accuracy. Isolated insect collections on plants do not provide information on insect abundance, utilization of other plants, and may not provide information about the kind of interaction, if any, the insect has with the plant. Many field plant-insect associations published are not true associations. Foster et al. (1981), for instance, listed 39 species of leafhoppers associated with woody snakeweeds (*Gutierrezia* spp.), however, at least 12 species were grass-feeding leafhoppers, and two were polyphagous. Studies like the later, based in isolated collections on single target plants, are not very useful to assess information on insect host ranges, plant-insect interaction or abundance estimation.

In this study, we analyzed host plant partitioning by a leafhopper guild in the Chihuahuan Desert. Our present work is an initial step toward evaluating the potential of using leafhoppers in augmentative biological control. Our work differs from previous studies in that we used resource selection methodology (Manly et al. 1993, Alldredge et al. 1998) to examine plant use patterns. Resource selection methods compare relative use and availability of resources (e.g., habitats). Plant utilization patterns of an insect guild on a plant community have been poorly studied. Some studies have examined entire guilds, but they have been based on geographical records of host plants (Claridge and Wilson 1981). Our study is unique because we have analyzed host plant partitioning by a leafhopper guild in the Chihuahuan Desert on several plant species simultaneously. Most studies in natural vegetation examine a single herbivore on several host plants (Alstad and Edmunds 1983), or many herbivores on one or two plant species (Denno 1977, Raupp and Denno 1979). Some of the Chihuahuan Desert plants we examined have economical importance because of their undesirable nature (*Gutierrezia* spp., *Flourensia cernua* DeCandolle, *Prosopis glandulosa* Torrey) and may be subject to control or management.

Materials and Methods

The study was conducted in a 150 by 50-m plot located on the piedmont slope of Doña Ana Mountains at the Chihuahuan Desert Rangeland Research Center site of New Mexico State University, Doña Ana County, NM, USA. The plant community is a shrubby-grassland dominated by creosote bush [*Larrea tridentata* (DeCandolle) Coville], woody snakeweeds (*Gutierrezia* spp.), honey mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*), creosote bush being the dominant plant. Climate in the sampling area is arid (Thornwaite 1948) characterized by an annual precipitation of 225 mm, ≈50% of which occurs between July and October, with a wide range of diurnal temperatures and low relative humidity (Buffington and Herbel 1965).

Sampling. The site was sampled on nine dates, from June of 1997 through July of 1998 (5 June 23 June 31 July 13 September and 11 November 1997; 31 January 11 May 21 June and 8 July 1998). Thirteen shrub, sub-shrub and perennial herb plant species (Table 1) were chosen for this study with the following criteria: (1) importance in the community in terms of abundance, (2) taxonomic variability (six plant families), and (3) variability in architecture and phenology.

Plant specimens were randomly selected in the following manner. Ten transects of 50 m each were randomly located across the plot. Thirteen points were randomly placed along each transect using a random number table. A plant species was randomly assigned to each of the 13 points and subsequently, a trap was placed in the specimen of the assigned species located closest to the point. In the case of *Croton pottsii* (Klotzsch) Mueller of Aargau, a very small plant that occurs in clumps, a single trap was placed among several plants. With this method, plants having a random or regular distribution had a higher probability of being selected relative to plants growing in patches. However, the method was chosen because it was time-effective and allowed us to place the traps during one morning. At each sampling date, a standard unbaited Biolure red delta prism-shaped sticky trap (Consep

Biorational Products for Agriculture, Bend, OR), measuring 10 by 18 cm on each of the three sides (540 cm^2 total), was placed one per plant sampled. These were located in each of 10 replications of the 13 plant species, resulting in a total of 130 sampled plants, with the following exception. On the first and second sampling dates, *Brickellia laciniata* was not sampled and only five replications per plant species were made. Traps were left to collect insects for 6 d, based on a prior pilot study that identified the length of time at which insect numbers collected stabilized.

In the laboratory, the sap-feeding insects were removed from the trap using a citric acid solution (Goo Gone, Magic America Corporation, Cleveland, OH) and identified. Nymphs were not included in this study due to the difficulty in identifying them. Mervin Nielsen (Brigham Young University, Provo, UT) identified all leafhopper subfamilies except Thyplobicinae, which were identified by Raymond Gill (Plant Pest Diagnostic Center, Sacramento, CA). Raymond Gill encountered several difficulties in identifying *Empoasca* species; in addition, no survey of this genus had been carried out in New Mexico. It was impracticable to identify all the *Empoasca* collected, so a sample of roughly 25% was identified for each plant species. To estimate plant specimen volume, specimen's length, width and height were measured after each trap was placed. Voucher specimens are deposited at the Arthropod Museum, New Mexico State University and at USDA ARS South American Biological Control Laboratory collection in Argentina. No voucher numbers are available at this time.

Statistical Analysis. Plant utilization was determined for the 13 most abundant leafhopper species using the Neu method (Neu et al. 1974). This method compares the availability of each plant species with the actual proportion used by the sap-feeding insects using a chi-square goodness-of-fit test. Critical assumptions are that all the insect observations are independent and that the availability of each plant is the same for all insects. In this study, plant availability was measured as the total volume of each plant species sampled. Our scientific hypothesis was that leafhoppers used plants differentially. Statistically, the null hypothesis tested states that leafhoppers use plants in proportion to plant availability, considering all the plants simultaneously. When this hypothesis was rejected, we examined plant use on each plant species separately using simultaneous confidence intervals. Confidence intervals for the proportion of use were calculated with a Bonferroni *t*-statistic as follows:

$$CI = \hat{p}_j \pm t_{\alpha/2,k.} \sqrt{\hat{p}_j (1 - \hat{p}_j)/n}$$

with $\hat{p}_j$ = proportion of plant species utilization by leafhopper species "*j*" and $t_{\alpha/2,k}$ is the *t*-distribution value with a pairwise comparison rate of 0.0039 to ensure that the $k = 13$ simultaneous confidence intervals have an overall 95% coverage (Kuehl 1994). When the lower limit of a confidence interval was negative, it was truncated to zero.

Small numbers of some insect species preempted the need for statistical testing in some cases. For example, when an insect did not use a plant species, the resulting confidence interval had no width, thus averting the need for a statistical test. Plants on which a leafhopper species was never detected were treated separately.

Three categories of plant usage by insects were established. Host avoidance was determined when leafhoppers were never found using these plant species, or insects used a plant species at a rate lower than availability, i.e., the upper confidence interval of the proportion used by the insect fell below plant availability. Host preference is defined as any positive deviation from arrangements made at random (Mackay and Singer 1982), i.e., the lower confidence interval of proportion used fell above plant availability. Plants were said to be randomly used when insects used the plant species in proportion to its availability, i.e., plant availability fell inside the confidence interval of estimated proportional use. Availability of host plants is difficult to quantify but refers here to the approximate volume of an individual plant, rather than to the total volume of a plant species in the study area. Behaviors like mating or avoidance of natural enemies were not discriminated in our analysis. When possible, we compared our findings to those reported in the literature for the same insect-plant species combinations).

To investigate seasonal plant utilization patterns, we built a matrix using leafhopper counts and the proportion of each leafhopper species use of each plant species for each of the four seasons. We also analyzed plant utilization temporal patterns of the leafhoppers in response to changes in leafhopper relative abundance. Leafhopper relative abundance was determined by comparing counts of each species by date to the maximum value detected for that species over all dates.

Results and Discussion

Thirty-seven leafhoppers species belonging to eight subfamilies were collected in the study area, most occurring in very low densities. The species of the Thyplobicinae *Empoasca* complex were the most abundant on most plant species. The overall average number of leafhoppers captured per plant was 1.7. Leafhoppers were captured in only 53.8% of the 1,030 individual plants sampled. If we only consider plants where leafhoppers were captured, the average increases to 3.2 leafhoppers per plant. Leafhopper detections (presence/absence) by plant species are listed in Table 2. No leafhopper species used all plants in proportion to their availability (Table 3), and all plants were preferred by at least one leafhopper, with the exception of *Prosopis glandulosa.*

Of the 169 possible plant-insect pairs (13 leafhoppers and 13 plants analyzed), 41.4% (70) demonstrated host avoidance, and 48.0% (82) demonstrated random use. Only 9.5% of the pairs (18) demonstrated specific plant preference. Nine leafhopper species (70% of the analyzed species) accounted for the 18 instances of plant preference (Table 4). Of these, six leafhoppers species were more abundant than expected in only one host

Table 2. Leafhoppers and plants where they were collected

Species	PI	BL	GS	RM	DF	FC	LT	PG	CP	YE	ML	ZA	TA
Subfamily Agalliinae													
Aceratagalia lyrata (Baker)	X	X		X	X			X	X		X	X	X
Aceratagalia uhleri (Van Duzee)			X		X				X	X	X		
Ceratagalia bigeloviae (Baker)			X		X	X			X	X	X		X
Subfamily Deltocephalinae													
Scaphytopius f. frontalis (Van Duzee)				X		X				X	X		
Scaphytopius f. nigricollis (Ball)			X	X	X	X	X	X		X			X
Scaphytopius f. heldoranus (Ball)			X	X		X						X	X
Flexamia sp.	X	X	X						X		X	X	X
Athysanus sp.												X	
Texananus latipex DeLong									X		X	X	
Opsius stactogalus Fieber								X					
Deltocephalus sp.	X			X	X	X	X	X	X		X	X	X
Mesamia coloradensis (Gillette & Baker)	X		X		X				X	X	X	X	X
Doleranus lucidus (Baker)	X	X	X	X	X	X	X	X	X	X			
Driotura vittatta Ball		X	X	X	X	X			X		X	X	
Spathanus acuminatus (Baker)	X	X	X	X	X	X	X	X	X	X	X	X	X
Exitianus exitiosus (Uhler)	X		X		X		X	X	X			X	X
Macrosteles major (Dorst)				X	X								
Ollarianus strictus (Ball)							X						
Ollarianus sp.								X					
Circulifer tenellus (Baker)				X	X	X	X	X	X	X	X	X	X
Acinopterus sp.		X											
Paraphlepsius sp.								X					
Balclutha sp.	X		X			X							X
Subfamily Cicadellinae													
Dikraneura sp.	X	X	X	X	X	X	X	X	X	X	X	X	X
Subfamily Gyponinae													
Ponana sp.		X	X			X		X	X	X	X	X	
Prairiana subta (Ball)													X
Subfamily Ledrinae													
Xerophloea peltata (Uhler)			X										
Subfamily Xestocephalinae													
Xestocephalus sp.		X			X							X	
Subfamily Typhlocybinae													
Empoasca spp.	X	X	X	X	X	X	X	X	X	X	X	X	X
E. acantha DeLong & Davidson	X	X		X		X				X		X	
E. bidens DeLong	X	X	X			X		X		X			
E. dilitara DeLong & Davidson		X	X	X		X		X		X		X	
E. cothurna DeLong and Davidson	X												
E. mexicana Gillette			X					X		X		X	X
E. abrupta DeLong	X	X											
E. cerea DeLong			X	X		X				X		X	X
E. calcara DeLong													
Subfamily Iassinae													
Parabolocratus sp.							X						

PI = *P. incanum*, BL = *B. laciniata*, GS = *Gutierrezia* spp., RM = *R. microphylla*, DF = *D. formosa*,FL = *F. cernua*, LT = *L. tidentata*, PG = *P. glandulosa*, CP = *C. pottsii*, YE = *Y. elata*, ML = *M. leucanthum*, ZA = *Z. acerosa*, TA = *T. acerosa*.

plant. *Spathanus acuminatus* (Baker), *Scaphytopius frontalis nigricollis* (Ball), and *Empoasca* spp. used more than one host plant species in greater proportion to their availability. *Spathanus acuminatus* appeared to have two biotypes with differences in plant utilization. One biotype used *L. divaricata* more than expected, and the other biotype used *L. divaricata* and *F. cernua* more than their availability.

Assuming that plant utilization reflects feeding patterns, and excluding the *Empoasca* complex, we found six (50%) leafhopper species that preferred only one plant species, two (16.7%) leafhoppers preferred two plant species, and four (33.3%) showed no preference for any plant.

Insects Exhibiting Preference in the Plant Utilization Pattern. Some plant-insect associations were highly specific. For example, >90% of *S. f. frontalis* (Van Duzee) were found on *Rhus microphylla* Engelmann. Sixty-one percent of *Aceratagallia lyrata* (Baker) were collected on *Croton pottsii;* 58% of *Dikraneura* sp. specimens were collected on *Dalea formosa* Torrey, and 44% of *Ceratagalia bigeloviae* (Baker) were collected on *Gutierrezia* spp.; *Mesamia coloradensis* (Gillette & Baker) (47%) used *Zinnia acerosa* (DeCandolle) Gray more than expected.

Two leafhoppers were found more often than expected on two host plants, *Scaphytopius frontalis nigricollis* and *Spathanus acuminatus.* Twenty-nine percent of *S. f. nigricollis* were collected on *L. tridentata* and 21% on *Yucca elata* Engelmann. *Scaphytopius f. nigricollis* did not exhibit changes in host plants over time, only using *L. tridentata* and *Y. elata* in summer and fall. The only host plant reported for *S. f. nigricollis*, previous to this study, was *L. tridentata* (Hepner

Table 3. Matrix showing positive (proportion of detected insect on that plant), avoided (−), and random (R) interaction between plants and leafhoppers in study area

Species	Total abundance	BL	CP	DF	FC	GS	LT	ML	PI	PG	RM	TA	YE	ZA
Empoasca spp.	773	0.20	0.02	R	0.09	0.17	(−)	0.02	0.22	(−)	(−)	0.02	R	R
Dikraneura sp.	203	(−)	R	0.58	R	R	R	R	R	(−)	(−)	R	R	R
S. acuminatus	138	(−)	R	R	0.12	R	0.44	R	R	(−)	(−)	R	R	R
S. f. nigricollis	61	(−)	(−)	R	R	R	0.29	(−)	(−)	(−)	(−)	R	0.21	(−)
A. lyrata	46	(−)	0.61	R	(−)	(−)	(−)	R	R	(−)	(−)	R	(−)	R
S. frontalis	44	(−)	(−)	(−)	R	(−)	(−)	R	(−)	(−)	0.91	(−)	R	(−)
M. coloradensis	30	(−)	R	R	(−)	R	(−)	R	(−)	(−)	(−)	R	(−)	0.47
Deltocephalus sp.	29	(−)	R	R	R	(−)	(−)	0.28	R	(−)	(−)	R	(−)	R
D. lucidus	26	R	R	R	R	R	R	(−)	R	R	(−)	(−)	R	(−)
C. tenellus	26	(−)	R	R	R	(−)	R	R	(−)	R	R	R	R	R
Ponana sp.	20	R	R	(−)	R	R	(−)	R	(−)	(−)	(−)	(−)	(−)	R
D. vittata	20	R	R	R	R	R	(−)	R	(−)	(−)	(−)	(−)	(−)	R
C. bigeloviae	18	(−)	R	R	R	0.44	(−)	R	(−)	(−)	(−)	R	R	(−)

BL: *B. laciniata*, CP: *C. pottsii*, FL: *F. cernua*, GS: *Gutierrezia* spp., LT: *L. tidentata*, ML: *M. leucanthum*, PI: *P. incanum*, PG: *P. glandulosa*, RM: *R. microphylla*, TA: *T. acerosa*, YE: *Y. elata*, ZA: *Z. acerosa.*

1947). Forty percent of *S. acuminatus* were collected on *L. tridentata* and 12% were found on *F. cernua.*

Biotypes of *Spathanus acuminatus.* Though considered monophagous on *L. tridentata* (Oman 1949, Ellsbury and Nielsen 1978, but see Richerson and Boldt 1995), this species used both *L. tridentata* and *F. cernua* more than expected in our study. However, we observed two biotypes in *S. acuminatus* (light and dark coloration) that exhibited differences in host use pattern and occurrence. Differences in coloration have been reported over all its distribution; these biotypes were attributed to age and degree of sclerotization (Ellsbury and Nielsen 1978).

Spathanus acuminatus dark biotype used *L. tridentata* (23.46%, CI = 0.0986–0.3705) and *F. cernua* (14.81%, CI = 0.0342–0.2621) more than expected, whereas the light biotype only preferred *L. tridentata* (62%, CI = 0.4421–0.8038). The light biotype occurred from the end of spring to midsummer with the highest counts between the end of June and beginning of July (Fig. 1). Its pattern of use of *L. tridentata* followed this occurrence curve, reaching its maximum in the summer of 1997. The dark biotype occurred throughout the year with very low counts in winter and highest detections in spring and fall (Fig. 1). The dark biotype used *L. tridentata* and *F. cernua* all year round, except in winter when this leafhopper was almost absent. Sympatric race formation and speciation in phytophagous insects has been previously documented (Bush 1969, 1975; Wood and Guttman 1981). It is possible that *S. acuminatus* is in the process of race formation, but further studies are necessary to confirm this hypothesis.

Empoasca Complex. Due to the difficulties in identifying the *Empoasca* species, we analyzed the genus *Empoasca* instead of each species separately. *Empoasca* spp. used five species of Asteraceae more often than expected: *Parthenium incanum* Humboldt, Bompland & Kunth (22%), *B. laciniata* (20%), *Gutierrezia* spp. (16%), *F. cernua* (9%), *elampodium Leucanthum* Torrey & Gray (2%). One member of the Euphorbiaceae, *C. pottsii*, was selected at a rate greater than availability, although because small size (volume ≈0.0003 m^3) and shape made volume measurements difficult, actual plant volume for this species may have been underestimated. Even though low insect numbers were detected on *C. pottsii and M. leucanthum*, their extremely low availability resulted in preferential use of these species.

Raymond Gill found that *Empoasca* spp. included at least eight species in the study area (Table 5). He found three groups that appeared to be composed of at least two intergrading species. The first group was an intergrading of specimens between *E. omani* Davidson & DeLong and *E. bidens* (DeLong) (=*E. bidens* in Table 2); the second group was composed of *E. bitubera* DeLong and *E. mexicana* Gillette (=*E. mexicana* in Table 2), species especially difficult to separate due to their morphological similarities. A third group was composed of species that apparently do not correspond to any described species. Table 5 shows that 86.49% of *E. mexicana* were collected on *Gutierrezia* spp., 72.97% of *E. acantha* on *B. laciniata. E. bidens* mainly used two host plants, 36.23% of *E. bidens* were collected on *F. cernua* and 47.83% on *P. incanum.*

Gandolfo and Richman (1996) found 11 leafhopper species associated with *Gutierrezia* spp. in New Mexico, among them *Empoasca bitubera* (=*mexicana*) and *E. neaspersa* Oman & Wheeler. *E. bitubera* (=*mexicana*) was the only species that completed its life cycle on *Gutierrezia* spp. (Gandolfo and Richman 1996). They observed that *Gyponana delta* Ball, and possibly *Ceratagalia bigeloviae*, fed on *Gutierrezia* spp. in the field. Interestingly, in our study, *C. bigeloviae* was positively associated with *Gutierrezia* and *G. delta* was never collected in the plot.

Insects Not Exhibiting Preference for Any Plant. Four leafhoppers (31% of the studied insects), *Ponana* sp., *Doleranus lucidus* (Baker), *Circulifer tenellus* (Baker), and *Driotura vittata* Ball did not use any of the 13 plants in the study area more than expected. These species exhibited random use or avoidance behavior for each of the 13 plants (Table 3). *Ponana* sp. used eight plant species (62%) in proportion to their availability (avoided five plants) and was collected

Table 4. Matrix of plant availability and interval estimate of plant use for leafhopper-plant species pairs where a preference was indicated

	Offer	Plant Size (m^3)	*Dikran eura* sp.	*S. acuminatus*	*S. frontalis*	*Empoasca* spp.	*M. coloradensis*	*A. lyrata*	*S.f. nigricollis*	*C. bigeloviae*	*Deltacephalus* sp.
B. laciniata	0.137	2.47				0.162–0.243					
C. pottsii	0.003	0.00				0.005–0.033		0.396–0.821			
D. formosa	0.007	0.13	0.487–0.685								
F. cernua	0.030	0.55		0.042–0.198		0.060–0.118					
Gutierrezia spp.	0.009	0.16				0.130–0.205				0.067–0.822	
L. tridentata	0.057	1.04		0.283–0.519					0.118–0.468		
M. leucanthum	0.002	0.04				0.005–0.033					0.023–0.529
P. incautum	0.011	0.19				0.181–0.265					
P. glandulosa	0.361	6.45									
R. microphylla	0.333	6.03			0.781–1.037						
T. acerosa	0.002	0.03				0.007–0.037					
Y. elata	0.045	1.11							0.051–0.362		
Z. acerosa	0.002	0.04					0.190–0.743				

Plant sizes are means with *Croton pottsii* individuals smaller than .01 m^3.

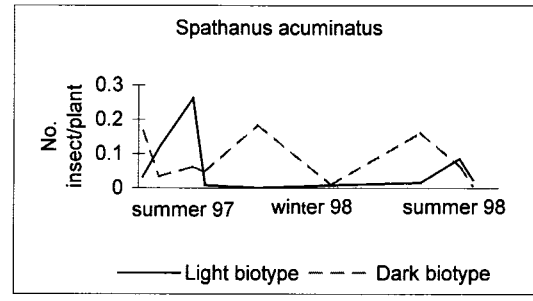

Fig. 1. Seasonal abundance of light and dark biotypes of *Spathanus acuminatus.*

mostly (75%) during spring. *Doleranus lucidus* used nine (69%) of the plant species in proportion to their availability and avoided four, being collected mostly (80%) during summer. *Circulifer tenellus* used 10 (77%) plant species in proportion to their availability, avoided three plant species, and was collected mostly (90%) in the fall. *Circulifer tenellus* has been documented to be a polyphagous leafhopper attacking desert plants in the fall and several crops in the summer (Severin 1933). *Driotura vitata* used seven (54%) plants species at random (avoided six) and was collected only during spring and summer.

Seasonal Patterns. Five leafhoppers showed maximum abundance in spring: *Dikraneura* sp., *Ponana* sp., *M. coloradensis*, and *S. f. nigricollis*, five in summer: *Empoasca* spp. *C. bigeloviae*, *D. lucidus*, *Deltocephalus* sp., and *D. vittata* and three had maximum abundance in spring and summer: *S. f. frontalis*, *S. acuminatus*, and *A. lyrata*, and one in fall, *C. tenellus.*

Generalist leafhoppers increased the number of plant species they used when leafhopper abundance increased. We did not detect seasonal qualitative patterns in plant utilization among specialist leafhoppers, i.e., insects did not vary in host plant species used. However, when they were more abundant, specialist insects used their preferred plants differently. We found two different functional responses to abundance increases. *Dikraneura* sp., *S. f. frontalis*, *A. lyrata*, *S. acuminatus*, and *Deltocephalus* sp. increased relative abundance on their preferred plants (Fig. 2), whereas specialist leafhoppers *C. bigeloviae*, *M. coloradensis*, and S. *f. nigricollis* decreased relative abundance on their preferred plants. Apparently, the former leafhopper group use their preferred plants more at the growing season when they are breeding. Overwintering adults use more plant species thereby decreasing use of their preferred plants. In turn, the latter leafhopper group specialized more during unfavorable seasons but less during the growing season and prefer to overwinter in one to two plants species (perhaps those plants offer a more suitable resource during unfavorable seasons).

Our analysis of plant utilization has two constraints, one inherent to the sample methodology used, and the other related to the ecosystem itself. The sticky-traps used were not selective in terms of plant use, therefore

Table 5. Partial identification of *Empoasca* complex, about 25% of the specimens, were identified

Host plant species	*E. acantha*	*E. bidens*	*E. dilitara*	*E. corthurna*	*E. mexicana*	*E. abrupta*	*E. cerea*	*E. calcara*	% identified	% collected
Z. acerosa	1	0	1	0	1	0	1	0	1.93	1.48
F. cernua	3	25	2	0	0	0	1	0	14.98	9.29
R. microphyllia	1	0	14	0	0	0	1	0	7.73	11.98
M. leucanthum	0	0	0	0	1	0	3	0	1.93	2.02
P. incanum	1	33	0	4	0	3	0	0	19.81	23.28
Gutierrezia spp.	0	1	6	0	32	0	6	0	21.74	17.50
L. tridentata	0	0	0	0	0	0	0	0	0.00	1.75
P. glandulosa	0	2	7	0	2	0	0	0	5.31	5.79
Y. elata	4	1	2	0	1	0	0	1	4.35	3.90
B. laciniata	27	7	9	0	0	3	0	0	22.22	21.13
D. formosa	0	0	0	0	0	0	0	0	0.00	1.88
Total	37	69	41	4	37	6	12	1	100.00	100.00

the insects sampled may or may not use the plant as a feeding source. Behaviors like natural enemy avoidance or mating may account for presence in the plant. In addition, insects may have been captured when jumping or flying by a plant, so that interaction with the plant was incidental.

Although we did not perform any preference studies (i.e., in which hosts are equally available) either in the laboratory or in the field, our results are consistent with information gathered by other researchers. Comparisons between available host records for eight (*Ceratagalia bigeloviae, Circulifer tennellus, Driotura vittata, Empoasca mexicana, Mesamia coloradensis, Scaphytopius frontalis nigricolis,* and *Spathanus acuminatus*) of the 13 studied leafhoppers showed 75% of similarity with our results (Ball 1907, Lawson 1928, DeLong 1932, Severin 1933, Hepner 1947, Ellsbury and Nielsen 1978, Gandolfo and Richman 1996). Differences in host use were strong enough to be detected despite the low number of collected leafhoppers. However, the test performed better for larger plants because it has a lesser ability to discriminate random use and avoidance when plant availability is small. Size differences among the plants studied were very high (between 0.0003 m^3, *C. pottsii* to 6.43 m^3, *P. glandulosa*).

In classical biological control it is essential to know insect host preferences (DeBach 1964, Harris and Zwolfer 1968, Harris 1974, Wapshere 1974), and laboratory preference tests are an obligate part of the protocol. Historically, lab tests were generally considered accurate when determining potential insect host ranges. However, some researchers stated that insect feeding on nontarget plants under laboratory conditions was not sufficient reason for rejection of potential biocontrol agents (Harris and Zwofler 1968, Wapshere 1989) because the physiological host range can differ from the ecological one. Wapshere (1989) suggested that the insects cannot follow all behavioral steps under laboratory conditions as they can under natural conditions, and therefore there may be a discrepancy between laboratory and field results. Claridge and Wilson (1978) demonstrated that leafhopper nymphs show less preference in laboratory feeding preference tests than in the field and some leafhoppers developed on plants that were not natural hosts. In addition, laboratory-determined host ranges of grass leafhoppers were much wider than natural ones (Whitcomb et al. 1994).

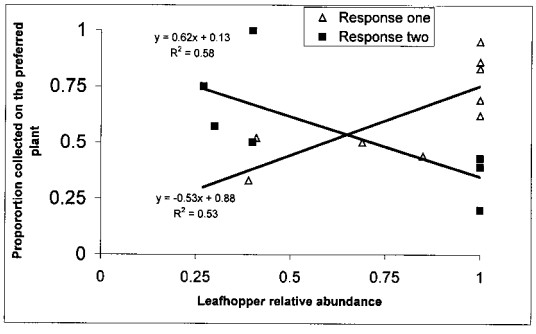

Fig. 2. Relationship between leafhopper relative abundance and and proportion of leafhoppers collected on their preferred plant.

Knowledge of insect field behavior regarding host plants is necessary when using native natural enemies for biological control, as well as insect population dynamics (Smith and Ueckert 1974) and plant usage patterns. Several plant species included in this study are considered undesirable, *Gutierrezia* spp., *L. tridentata, P. glandulosa,* and *F. cernua.* All plant species analyzed with the exception of *P. glandulosa* were preferred by at least one leafhopper species.

We suggest that field studies on insect plant utilization patterns using resource selection methods (Alldredge et al. 1998) may provide useful information on ecological host plant ranges, and could be included in studies of augmentative biological control. This is especially important in regard to leafhoppers, many of which have more than one host plant and thus cannot be assumed to be major biological control agents simply because they were found feeding on the target weed. Also, some occasional or temporally limited feeders on a specific weed could have a larger impact if they transmitted a pathogen and thus knowledge of their other hosts could be very useful. Once a weed is identified as a target for augmentative biological control, the current methodology could be used to identify native candidates for this control. A criterion to select the set of plant species to be sampled could be

determined by the centrifugal phylogenetic method (Wapshere 1973, 1974). Further work is needed to establish how an insect-plant community is assembled, to identify the various factors affecting insect abundance, and the types of interaction between its members.

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